

Doug., *M. primuloides* Benth., and *M. bioletti* Eastw. were used to represent section *Paradanthus*. Six different reciprocal crosses were attempted using an average of five flowers each. A *Paradanthus* intrasectional combination of *M. moschatus* and *M. floribundus* Dougl. produced vigorous but sterile F₁ hybrids. We have obtained only one chromosome count for this section: *M. moschatus*, $n = 16$ (unpublished).

On the basis of these genetic and cytological results we believe that the most natural taxonomic treatment is to group the three taxa, *M. cardinalis*, *M. verbenaceous*, and *M. lewisii*, in section *Erythranthe*. This treatment follows that of Pennell (1951) rather than that of Grant (1924) where *M. lewisii* is placed in section *Paradanthus*.

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TWO NEW SPECIES OF PENSTEMON IN COLORADO

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Since the treatment of *Penstemon* for Harrington's "Manual of the Plants of Colorado" was prepared, additional collections and study have made it necessary to recognize the following two new species for the state.

Penstemon harringtonii sp. nov. Herba perennis, glabra, 3- dm. 7 alta; caulibus erectis, simplicibus, glaucis; foliis glaucis, integris, crassis, obtusis vel acutis, mucronatis, basalibus spathulatis vel oblanceolatis, 5-7 cm. longis, 1.5-2.5 cm. latis, caulinis ceteris parvioribus, sessilibus, obovatis, elliptico-ovatis vel cordato-amplexicaulibus, ad inflorescentiam versus gradatim reductis; thyrso cylindraceo, angusto, interrupto, 5-10-fasciculato; calyce 5-9 mm. longo, lobis ovato-lanceolatis, acutis vel acuminatis, scarioso-marginatis; corolla 18-24 mm. longa, coerulea (vel rosea), bilabiata, fauce ampliata; staminibus didynamis, inferioribus

corollae faucem multo excedentibus; antheris 2.5–3 mm. longis, glabris, sagittatis; loculis antherarum de apice ad basim dehiscentibus, confluentibus, haud explanatis; filamentis sterilibus dilatatis (usque ad 1–1.5 mm. latitudine), pilis 1–2 mm. longis, dense aurato-barbato; capsulis ignotis.¹

Glabrous perennial, 3–7 dm. tall; stems one to few, simple, erect, glaucous below, often purplish, especially above; leaves entire, thickish, glaucous, mucronate, the basal 1.5–2.5 cm. wide, 5–7 cm. long, spatulate to oblanceolate, obtuse to acute, the lower cauline 1–2 cm. wide, 2–5 cm. long, obovate, elliptic or ovate, acute, the upper cauline gradually reduced, ovate to cordate-clasping; inflorescence cylindrical, of 5–10 rather lax-flowered fascicles, one-third to one-half or more the height of stem; peduncles surpassing bracts, especially above; bracts all acute, scarious-margined, the lower broadly sessile-clasping, the upper reduced and inconspicuous, longer than wide; calyx 5–9 mm. long, the lobes ovate- to lance-acuminate, striate, narrowly scarious-margined; corolla 18–24 mm. long, pale to deep coerulean blue, often lilac-tinged on tube, or strongly pinkish-lilac throughout, the throat ampliate-funnelform, rather distinctly bilabiate, the lower lobes divergent but scarcely reflexed, the upper arched-erect; stamens conspicuously didynamous, the upper pair attached to corolla at its very base, the lower pair attached along corolla tube for about one-half their lengths, the free part then curved ventrally in the throat and well-exserted outward and upward to bring anthers opposite middle of orifice of corolla; anthers 2.5–3 mm. long, glabrous, sagittate, attached to filament at their middle or below, the connective wide, the sacs conjoined for one-half or more of their lengths, dehiscing throughout but not explanate, remaining parallel but curved; staminode glabrous to middle, then abruptly densely bearded with golden yellow hairs, those on the upper surface 1–2 mm. long, those on the lower surface prominent, but shorter and less dense, the staminode widened distally to 1–1.5 mm., rounded at tip and curved ventrally, usually a little exserted from orifice of corolla tube; mature capsules not seen.

Type. Abundant in sagebrush, altitude about 8000 feet, 3–5 miles northwest of Green Mountain Dam, Grand County, Colorado, 19 June 1952, *Penland 4296* (COCO; isotypes, COLO, CS, GH, NY, RM, UC, US).

Other known collections. COLORADO. Eagle County: rather dry slope 5 miles east of Wolcott, elevation 7200 feet, 7 June 1951, *H. D. Harrington 4935* (COCO, CS). Routt County: pinyon, cedar, sage association, elevation 7500 feet, 2 miles north of McCoy, Highway 131, 29 June 1951, *M. & C. Norton s.n.* (COCO, CS).

Penstemon harringtonii is readily recognized both in the field and in the herbarium by its two well-exserted stamens (fig. 1), a character that appears remarkably constant. Judged on the basis of its anthers it is most closely related to *P. cyathophorus* Rydberg, and it is therefore referred to the section *Coerulei* (as defined by Pennell, 1935). It differs

¹ The assistance of Mr. Robert M. Ormes in preparation of Latin diagnoses is gratefully acknowledged.

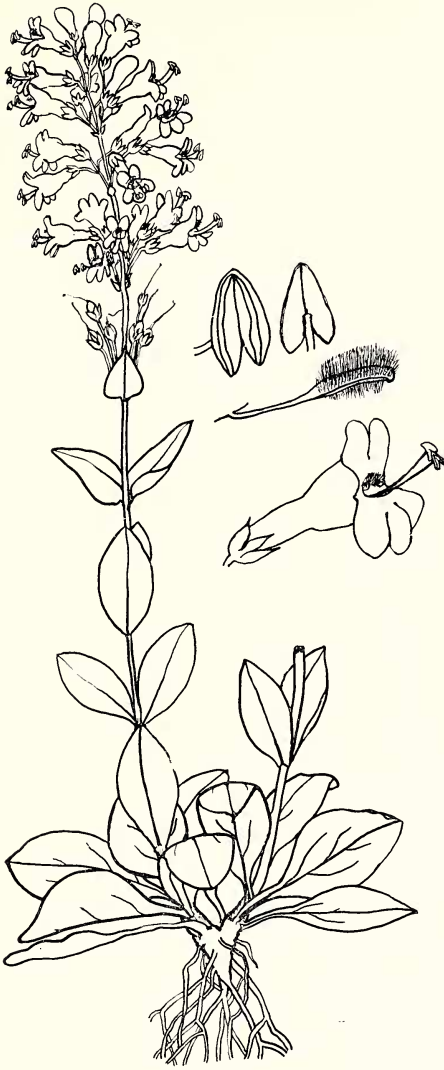


FIG. 1. *Penstemon harringtonii*. Habit, ca. $\times \frac{1}{8}$; anthers, $\times 5$; staminode, ca. $\times 1\frac{1}{2}$; flower, $\times 1$.

from *P. cyathophorus* in its larger flowers (18–24 mm. long as compared to 9–15 mm.), in having only two instead of its four stamens strikingly exerted, in its longer anthers (2.5–3 mm. as compared with 2 mm.), and in its strongly reduced bracts, which are mostly longer than broad (the reverse is true of *P. cyathophorus*). In general appearance, however, *P. harringtonii* is more like *P. osterhoutii* Pennell (same section), to which it

was first referred, than it is like *P. cyathophorus*. Although the flowers average 14–20 mm. long in *P. osterhoutii*, thus approaching those of *P. harringtonii*, the anther sacs are widely divaricate and not at all sagittate as in *P. harringtonii*, and the stamens are not or scarcely exerted in *P. osterhoutii*. These closely related species may be keyed as follows:

Anthers sagittate with parallel sacs; 2 or all 4 stamens well-exserted.

Flowers 18–24 mm. long; only 2 stamens exerted; anthers 2.5–3 mm. long; bracts mostly longer than broad.....*P. harringtonii*

Flowers 9–15 mm. long; all 4 stamens exerted; anthers 2 mm. long; bracts mostly broader than long*P. cyathophorus*

Anthers with sacs divaricate; stamens not or scarcely exerted.....*P. osterhoutii*

The three cited collections of *P. harringtonii* represent a distribution of this plant on both sides of the Colorado River drainage system, and, to the south, on both sides of the Gore Range (Eagle and Blue rivers). The known range of *P. cyathophorus* (Grand and Jackson counties in Colorado, and in adjacent southern Wyoming) is to the north of that of *P. harringtonii* (Eagle, Grand, and Routt counties, Colorado), although at one place in Grand County the two species occur within 2–3 miles of each other. *Penstemon osterhoutii*, the other species closely related to *P. harringtonii*, is common to the west of *P. harringtonii* in Eagle and Garfield counties, but the ranges of the two do not overlap. Moreover, *P. harringtonii* occurs at elevations of 7200–8000 feet, while *P. osterhoutii* has not been collected above an elevation of 6600 feet.

The unusually interesting *Penstemon acaulis* Wms. was first collected in Sweetwater County of southwestern Wyoming. Later it was found in adjacent Daggett County in Utah. So far as is known it has not been reported from south of the Uinta Mountains in Utah, or from the northwestern corner of Colorado. In 1951 the writer collected a *Penstemon* which was at first presumed to be only a more robust form of *P. acaulis*. It was found a few miles east of Elk Springs, south of the Yampa River in Moffat County, Colorado, a locality approximately eighty airline miles southeast of the nearest known station for *P. acaulis*. In order to secure better diagnostic material this area was again visited in 1952 and 1953. In those years two additional stations for the plant were discovered; both of these were north of the Yampa River, between Greystone and the Little Snake River. The collections and all material observed in the field are quite uniform in aspect, and continued study has led to the proposal of the following new species, whose closest relative is clearly *P. acaulis*.

Penstemon yampaensis sp. nov. Herba caespitosa perennis, 3 cm. vel minus alta; rhizomatibus ramosis; foliis 15–30 mm. longis, 2–4 (–5) mm. latis, oblanceolatis, acutis, cinereis, spiculato- vel papillato-pubescentibus, plus minusve viscidis; calyce 5–9 mm. longo, viscido-pubescente, lobis acuminatis, inferne scarioso-marginatis; floribus 2–4 in ramo terminali; corolla 15–18 mm. longa, pallide roseo-purpurea (vel demum coerulea), extus glanduloso-pubescente, basi faucis rotundatae haud pli-



FIG. 2. *Penstemon yampaensis* (Penland 4415). About $\times 1$.

catæ aliquantulo ventricosæ aureo-barbata, lobis posterioribus quam ceteris brevioribus; staminibus inclusis; loculis antherarum 1–1.5 mm. longis, glabris, confluentibus, haud late explanatis; filamentis sterilibus paulo exserto, insuper aureo-barbato; capsulis fere globosis, 4 mm. longis, glabris; seminibus 2–4, nigris, lunatis, rugosis.

Caespitose, essentially acaulescent perennial, spreading from branching rootstocks and in the open forming loose mats up to one foot in diameter, 3 cm. or less in height; leaves cineraceous, 15–25 (–30) mm. long, 2–4 (–5) mm. wide, oblanceolate, acute but not mucronate, scabro-pubescent with low, blunt, papilliform hairs (common on upper portion) or longer, straight or somewhat recurved, spiculate hairs (common toward base and petiole), the foliar hairs not gland-tipped but evidently viscid; mid-rib and two or more lateral veins prominent on dried specimens; flowers usually 4 (2–6) on each of the very short ultimate branches, often exceeded by the foliage; calyx 5–9 mm. long, the lobes long-acuminate, rather densely viscid-pubescent, narrowly scarious-margined below; corolla 15–18 mm. long, lilac, or with strong bluish tinge when older (?), on dried specimens usually blue, glandular-pubescent externally, golden- (to whitish-) bearded in throat below, the two upper lobes arched-erect, but little shorter than the less divergent three lower lobes (which may reach a length of 5 mm.), the throat moderately ampliate above short tube, some-

what ventricose, not at all plicate; stamens with longer pair reaching limb of corolla, the anther sacs 1–1.5 mm. long, ovate to oblong-ovate, glabrous, minutely denticulate along suture, divaricate, dehiscent confluently, not explanate; the staminode exerted from throat, bearded all along its dorsal surface with golden hairs, a little widened distally (to as much as 0.75 mm.), the apex emarginate; capsules nearly globose, about 4 mm. long, glabrous at maturity; seeds lunate, 2–3 mm. long, black, rugose and punctulate, 2–4 per capsule.

Type. Sandy, calcareous knoll, scattered grass and sage; 5.5–6 miles east of Elk Springs, Moffat County, Colorado, 9 June 1953, *Penland 4415* (COCO; isotypes, COLO, GH, NY, RM, UC, US). All other collections are from Moffat County, Colorado: type locality, 26 June 1951, *Penland 4236* (topotype, COCO); type locality, 20 June 1952, *Penland 4311* (topotypes, COCO, COLO, CS, GH, NY, RM, UC, US); 20 miles south of Vermillion Creek Bridge, 22 June 1952, *Penland 4326* (COCO, UC, US); 3–4 miles south of Greystone, 10 June 1953, *Penland 4426* (COCO, NY, RM).

A key serving to separate *P. acaulis* (fig. 3) and *P. yampaensis* (fig. 2) follows:

Leaves essentially linear, 1–1.5 mm. wide, 10–20 mm. long; flowers 1 (–2) per ultimate floriferous shoot; corolla 14–16 mm. long, blue.....	<i>P. acaulis</i>
Leaves oblanceolate, 2–4 (–5) mm. wide, 15–25 (–30) mm. long; flowers usually 4 (–6) per ultimate floriferous shoot; corolla 15–18 mm. long, lilac to bluish-lilac	<i>P. yampaensis</i>

The foliar pubescence of these two species is essentially the same, though more of the spiculate hairs seem to be present in *P. yampaensis*, especially toward the leaf base. *Penstemon acaulis* was assigned to the section *Caespitosi* by Williams in his original description of this species (1934). Keck (1937) also assigned it to this group but changed the rank of the group to a subsection of the section *Ericopsis*. Keck pointed out, however, that in *P. acaulis*, "The character of its pubescence is unique in this group of species." There are two probable reasons for this uniqueness: 1) the papillate hairs, besides being short and blunt, are very broad at the base (commonly 44–73 microns, as compared to 14–25 microns for hairs of *P. caespitosus* Nutt., *P. crandallii* A. Nels., *P. retrorsus* Payson and *P. abietinus* Pennell, all of which Keck also places in the *Caespitosi*; 2) the external walls of these hairs in *P. acaulis* and *P. yampaensis* are smooth or nearly so, while those of the four species named just above are denticulate (as observed in boiled or cleared material, at 100 × magnification). In this connection it is of interest that the hairs of *P. moffatii* Eastw. (section *Aurator*) are also blunt and smooth-walled. Also, the apex of some leaves of *P. moffatii* may even show the papillate condition of *P. acaulis*, but the longer, blunt, recurved type of hair is typical for the species.

The midrib of leaves of dried specimens of both *P. acaulis* and *P. yampaensis* is prominent nearly throughout; in addition, *P. yampaensis* shows

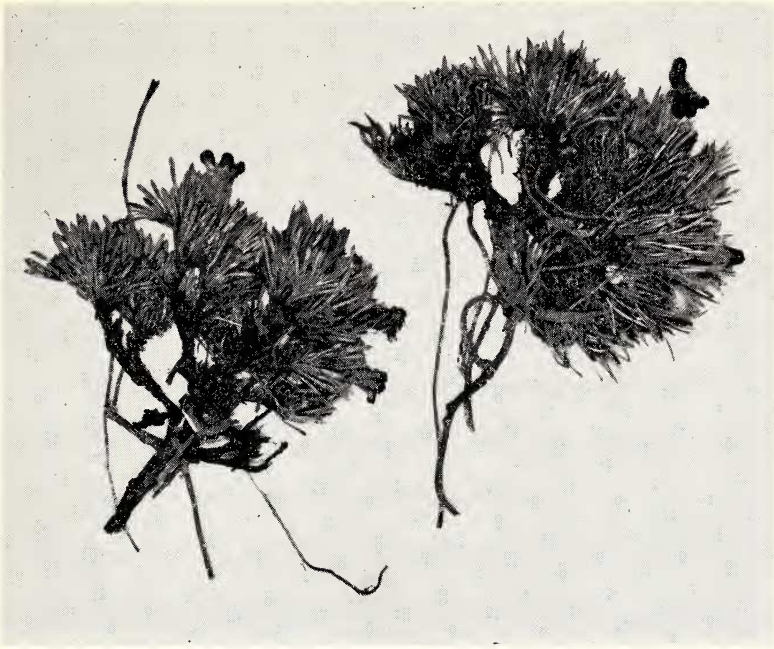


FIG. 3. *Penstemon acaulis* (Penland 4419). About $\times 1$.

two or more prominent lateral veins. This type of veining is certainly rare in the *Caespitosi*. Although the midrib may be prominent, as in *P. crandallii*, this condition is found only in the petiolar portion of the leaf. In fact, I have found a leaf situation similar to *P. yampaensis* in only one other case, a specimen from the Uinta Mountains of Utah which I have doubtfully referred to *P. abietinus*. Two other collections of *P. abietinus* show leaves agreeing with the other *Caespitosi*. (I have not studied leaves of *P. thompsoniae* (Gray) Rydb., however.) The midrib of *P. yampaensis* is not only prominent but is also relatively large (sometimes over 400 microns in diameter in cleared material, as compared with under 200 microns in *P. caespitosus*). Probably correlated with the presence of large lateral veins in *P. yampaensis* is the fact that a number of leaves have been found showing 1-4 small teeth near the apex.

The non-plicate character of the corolla throat certainly poses a question as to the assignment of *P. acaulis* and *P. yampaensis* to the subsection *Caespitosi*, where their caespitose nature would apparently place them. In all the other six species of the subsection (Keck, *loc. cit.*), the 2-ridged and commonly laterally flattened, plicate throat is a constant and diagnostic feature. Nor do *P. acaulis* and *P. yampaensis* fit into the other two subsections of *Ericopsis* (*viz.*, the *Linarioides* and the *Laricifolii*). It seems to me that their affinity is rather with the section *Aurator*, through such species as *P. nanus* Keck, *P. dolius* Jones, *P. pumilus* Nutt., and *P.*

moftatii Eastw. Perhaps the least that can be said for them is that they help to emphasize more strongly the relation between the sections *Aurator* and *Ericopsis*, a point which was elucidated by Keck.

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PECULIARITIES OF THE COLUMBIA RIVER GORGE FLORA

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The gorge cut through the Cascade Range by the Columbia River as it flows westward between Washington and Oregon has long been recognized as a place of peculiar botanical interest. If one studies the distribution of the plant species found there, he is soon impressed by the large number that are either endemic to the area or occur as isolated populations significantly removed from their normal range. My interest in the history of the various elements of the Pacific Northwest flora led me to speculate upon the meaning of these peculiar distributional patterns. It seemed possible that an analysis of them might furnish clues to the rôle the Columbia Gorge has played in the migrations of vegetation in the past. Its physiography and geographical relationship to adjacent vegetation areas would in themselves lead one to believe that it might have served as a pathway for the migration of many types of organisms. With this in mind, I have spent considerable time during the past few summers studying the local distribution of those plant species occurring within the Gorge. This field work has subsequently been supplemented with herbarium studies on their wider distribution. The present paper is the result of this work.

The species listed herein by no means constitute a complete flora of the Columbia Gorge, although I have tried to make the lists as inclusive as possible. The collections of other botanists who have collected extensively here have also been studied, particularly those of Howell, Gorman, Henderson, Suksdorf, and Sheldon. Nevertheless, further search would undoubtedly reveal more species which might be included in the roster. However, I am confident that the list is sufficiently extensive to give us a good general picture of the significant features of the Gorge flora as a whole, its distribution in the various habitats, and its relation to outside populations, which was the chief purpose of this investigation. Any additions to the number of species will not increase the accuracy of a study made from this particular viewpoint.